



Root Gravitropism and Below-ground Competition among Neighbouring Plants: A Modelling Approach

GERARDO RUBIO†‡, TOM WALK†, ZHENYANG GE†§, XIAOLONG YAN||, HONG LIAO|| and JONATHAN P. LYNCH*†

†Department of Horticulture, The Pennsylvania State University, University Park, PA 16802, USA, ‡Faculty of Agronomy, University of Buenos Aires, Buenos Aires, Argentina, §College of Engineering, South China Agricultural University, Guangzhou 516042, P. R. China and ||Root Biology Center, South China Agricultural University, Guangzhou 516042, P. R. China

Received: 9 July 2001 Accepted: 1 August 2001

Competition for nutrients among neighbouring roots occurs when their individual depletion volumes overlap, causing a reduction in nutrient uptake. By exploring different spatial niches, plants with contrasting root architecture may reduce the extent of competition among neighbouring root systems. The main objectives of this study were: (1) to evaluate the impact of root architecture on competition for phosphorus among neighbouring plants; and (2) to compare the magnitude of competition among roots of the same plant vs. roots of neighbouring plants. *SimRoot*, a dynamic geometric model, was used to simulate common bean root growth and to compare the overlap of depletion volumes. By varying the gravitropism of basal roots, we simulated three distinct root architectures: shallow, intermediate and deep, corresponding to observed genetic variation for root architecture in this species. Combinations of roots having the same architecture resulted in more intense inter-plant competition. Among them, the deep-deep combination had the most intense competition. Competition between deep root systems and shallow root systems was only half that of deep root systems competing with other deep root systems. Inter-plant root competition increased as soil diffusivity increased and the distance among plants decreased. In heterogeneous soils, co-localization of soil resources and roots was more important in determining resource uptake than inter-plant root competition. Competition among roots of the same plant was three- to five-times greater than competition among roots of neighbouring plants. Genetic variation for root architecture in common bean may be related to adaptation to diverse competitive environments.

© 2001 Annals of Botany Company

Key words: Root architecture, phosphorus, competition, common bean, *Phaseolus vulgaris* L. nutrient uptake, gravitropism.

INTRODUCTION

Interactions among plants occur in both natural and cultivated ecosystems and constitute an important determinant of the dynamics and structure of plant communities (Tilman, 1988). Although positive interactions ('facilitation') among plants exist (Callaway and Walker, 1997), resource competition is of paramount importance in many plant communities (Martin and Snaydon, 1982; Aerts, 1999). Competition among plants occurs both above- and below-ground. Whereas above-ground competition involves one principal resource (light), below-ground competition encompasses a broader spectrum of resources, including water and all the essential mineral nutrients. Several studies have shown that below-ground competition can be stronger and can involve more neighbours than above-ground competition (Casper and Jackson, 1997 and references therein).

Below-ground competition among neighbouring roots for diffusion-mobile nutrients occurs when their individual depletion volumes overlap, causing a reduction in nutrient uptake (Robinson, 1991). In contrast to nutrients such as nitrate that move via the mass flow of soil water, the notion

of depletion volumes fits better with nutrients that move primarily through diffusion, such as phosphorus. At root densities often encountered in soil, the entire root zone is almost depleted of nitrate unless replenished by mineralization or fertilization, and nitrate supply to plants normally includes soil volumes not included in the rooted layer (Jungk and Claassen, 1997). In the case of diffusion-mobile nutrients, uptake at the root surface creates a concentration gradient which drives diffusive flux to the root, progressively depleting the amount of nutrient in the rhizosphere. The radius of this depletion zone has been defined as the distance at which the nutrient concentration is at least 10 % less than its concentration in the bulk soil (Nye and Tinker, 1977). Since the width of this radius is a function of the diffusion coefficient, the concentration of the nutrient in the soil, and time, roots can be competing for some nutrients but not for others.

Since the pioneering theoretical works of Nye and Tinker (1977) and Baldwin (1976), relatively little research has addressed the mechanisms by which the depletion zones of neighbouring plants overlap and interact with each other. One obstacle is that it is difficult to detect nutrient gradients with the precision required to define the spread and the

* For correspondence. Fax 814 863 6139, e-mail jp14@psu.edu

eventual overlap of the depletion volumes, especially in a three-dimensional context. Models developed by Barber (1995) or Smethurst and Comerford (1993) are able to estimate depletion volumes in isolated or competing plants, assuming a homogeneous root distribution in the soil, but do not consider unevenly distributed roots. In this regard, geometric modelling may offer a useful alternative of numerically estimating depletion volume and depletion volume overlap in complex root systems. Recently, Hutchinson (2000) compared 2D and 3D models and concluded that completely different conclusions may be drawn by using 2D models instead of more realistic 3D models. In a 3D arrangement, the network of roots occupies a large volume of soil, so the roots are 'diluted' in space and the probability of overlap is reduced. A number of geometric models of root growth have been developed (e.g. Diggle, 1988; Pages *et al.*, 1989; Clausnitzer and Hopmans, 1994; for a review see Lynch and Nielsen, 1996). In the present study we used *SimRoot*, a dynamic 3D geometric model of root growth and architecture (Lynch *et al.*, 1997), to examine factors that can influence competition among neighbouring roots for phosphorus. In a previous study we used this model to examine competition among roots of the same plant (Ge *et al.*, 2000). Here, we extend that analysis by comparing the overlap of depletion volumes of competing plants.

Many factors can influence root competition for phosphorus, including root architecture, or the spatial configuration of a root system (Fitter *et al.*, 1991; Lynch, 1995). The relative immobility of phosphorus in soil makes its acquisition very dependent on soil exploration in time and space (Barber, 1995). Root gravitropism and branching are two primary components of root architecture. Since phosphorus availability is normally highest at the soil surface and decreases with depth (Pothuluri *et al.*, 1986), a shallower root system may be more competitive or advantageous for phosphorus acquisition. Modelling in *SimRoot* showed that shallower root systems are inherently more efficient for phosphorus acquisition, since roots are dispersed over a larger area and thus have less intra-plant root competition, while in stratified soils the shallower roots are better at exploiting localized nutrient resources (Ge *et al.*, 2000). However, in natural communities and in agroecosystems, shallower roots may also experience greater competition from neighbouring plants, especially in monogenetic stands where all plants have shallow roots. The effective diffusion coefficient (D_e) for phosphate largely determines the mobility of the nutrient in the soil, and thereby depletion zone volumes and competition among neighbouring roots. In a previous study we found that increasing D_e from 10^{-9} to 10^{-7} led to an expansion of the size of the depletion volume and, consequently, to greater overlap among roots of the same plant (Ge *et al.*, 2000). The distance between plants and the number of neighbouring plants may also affect root competition. It would be reasonable to assume that root competition for phosphorus increases with decreasing distance between plants, and with an increasing number of neighbouring root systems, although experimental evidence is needed to verify and quantify this relationship.

Firn and Digby (1997) introduced the concept of 'gravitropic set-point angle' (GSA), the angle at which any plant organ grows as a result of gravitropism. This angle is variable and is controlled by the developmental stage of the plant and by environmental factors. In the case of roots, the conjunction of the GSAs of every component of the root system ultimately defines the degree of shallowness of the whole root system. Taking into account the concept of GSA, in this paper we consider root gravitropism as the tendency of the root system to grow with a certain angle with respect to gravity. The objectives of this study were: (1) to evaluate the impact of root architecture on competition for phosphorus among neighbouring plants; and (2) to compare the magnitude of competition among roots of the same plant vs. roots of neighbouring plants.

MATERIALS AND METHODS

Effect of competition on the radial distribution of basal roots

Individual plants of common bean (*Phaseolus vulgaris* L.) tend to distribute their basal roots rather evenly around the centre of the plant. However, the presence of neighbours could change the radial distribution of basal roots (Schenk *et al.*, 1999). To assess this possibility, a glasshouse experiment was performed to evaluate whether the presence of neighbouring plants affects the radial distribution of basal roots. Common bean plants were grown in 20 l containers with solid-phase-buffered pure silica sand (Lynch *et al.*, 1990) providing a constant availability of low (1 μM), medium (10 μM) and high (30 μM) P in the soil solution. Plants of two genotypes (BAT 477 and DOR 364) were grown for 28 d in a temperature controlled (22–30 °C) glasshouse in University Park, Pennsylvania, USA. Plants were grown at one of three levels of competition (no competition, competition with a plant of the same genotype and competition with a plant of a different genotype) and P supply (low, medium and high). Competition treatments involved two plants per container, placed 5 cm apart. Five containers were randomly assigned to each treatment. The effect of the treatments on the radial distribution of basal roots was estimated after the percentage of roots in a 90° quadrant adjacent to the neighbouring plant (covering 25 % of the total area surrounding the stem, called here 'target area') was measured (Fig. 1). The percentage of roots in the 'target area' was determined as the proportion of the number of intersections of basal roots with a plastic mesh located 6 cm below the soil surface over the total number of intersections (Fig. 1). For treatments without competition, the 'target area' was calculated as the number of interceptions of the basal root with the plastic mesh on a 90° quadrant around the stem. For competition treatments, a line was traced between the two competing plants, and the 90° quadrant was located along the line (45° each side), covering the 'target area' (Fig. 1). In the non-competition treatment the quadrant was placed randomly. Results were tested for departure from uniform root distribution. Uniform distribution is represented when 25 % of the roots are in the 'target area'.

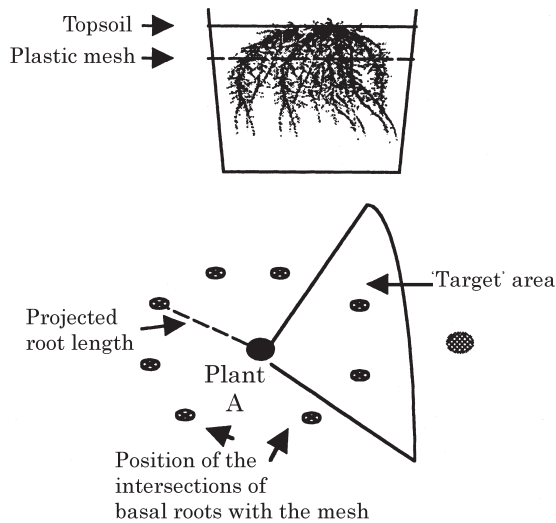


FIG. 1. Scheme of the procedure followed to evaluate the pattern of radial distribution of basal roots of common bean seedlings. The percentage of roots in the 90° quadrant closest to the neighbouring plant was determined from the proportion of the number of intersections of basal roots with a plastic mesh located 6 cm below the soil surface vs. the total number of intersections. In treatments without competition, the number of interceptions on a quadrant randomly located around the stem was counted. This quadrant has an angle of 90°, so that it covered 25% of the total area around the stem. In treatments with competition, a line was traced between the two competing plants, and the 90° quadrant was located along the line (45° each side), covering the 25% closest to the neighbouring plant ('target area').

Field study

From previous work (Liao *et al.*, 2001) we selected two common bean genotypes, one with a shallow root system (G19833) and one with a deep root system (DOR 364). The experimental site was located near Guangzhou in Guangdong Province, People's Republic of China (26°06'N, 113°15'E). The soil was a sandy loam with 6.1, 1.9 and 0.9 mg kg⁻¹ of available (Bray II) phosphorus in the top 0–10, 10–20 and 20–30 cm, respectively. The soil was mixed with lime (1500 kg ha⁻¹) 2 weeks before fertilization. The experimental design included two factors: phosphorus and competition. The phosphorus treatments were high phosphorus, in which 160 kg P ha⁻¹ was added as triple superphosphate, and medium phosphorus, without phosphorus addition. Phosphorus fertilization raised the

phosphorus content in the soil to 49.5, 2.25 and 2.8 mg kg⁻¹ of available (Bray II) phosphorus in the top 0–10, 10–20 and 20–30 cm, respectively. Both treatments received 180 kg N ha⁻¹ as urea and 200 kg K ha⁻¹ as KCl. The competition levels were G19833 in monoculture, DOR 364 in monoculture, and both genotypes in competition (genotypes intermixed by alternate planting within a row, so each plant has two neighbours of the other genotype). Seeds were planted 5 cm apart in all treatments. The study site was divided into five blocks, each one containing a randomized arrangement of the two phosphorus treatments and the three competition treatments. Seventeen days after transplanting, plant shoots were harvested and dry weights obtained after drying for 3 d at 60 °C.

Root distribution in the soil profile was analysed following a modified version of the profile wall method described by Schuurman and Goedewaagen (1971). Tangential trenches were dug 10 cm away from the row of plants. The walls were carefully scraped with a screwdriver to reveal the tips of the roots. Plastic transparent sheets (21.5 × 27.9 cm) were positioned adjacent to the exposed soil wall. The tips of the cut thick roots were mapped with a marker on the sheets. These thick roots represent the main axes of the basal roots, from which the fine roots develop.

Description of the multiple root system model

The dynamic geometric model *SimRoot* (Lynch *et al.*, 1997) was used to simulate root growth and architecture. The model was modified slightly to include factors involved in competition among multiple root systems. The new subprograms were implemented in C on an SGI 320 Workstation with dual 550 MHz Pentium III CPUs and 224 Mb RAM (SGI, Mountain View, CA, USA). The data file input is similar to that in *SimRoot* (Lynch *et al.*, 1997). In this study, three different root architectures, including shallow, deep and intermediate basal roots (Fig. 2), were generated. The root growth parameters for the intermediate root system were taken from field-grown *Phaseolus vulgaris* 'Carioca' (Lynch and van Beem, 1993), the range of deeper and shallower root systems were based on observations of other genotypes (e.g. Bonser *et al.*, 1996). The program generates total cylinder depletion zone data for all of the competing root systems. The basic algorithm of this program is constructed by adding the cylinder depletion zone of neighbouring root systems to that of the subject

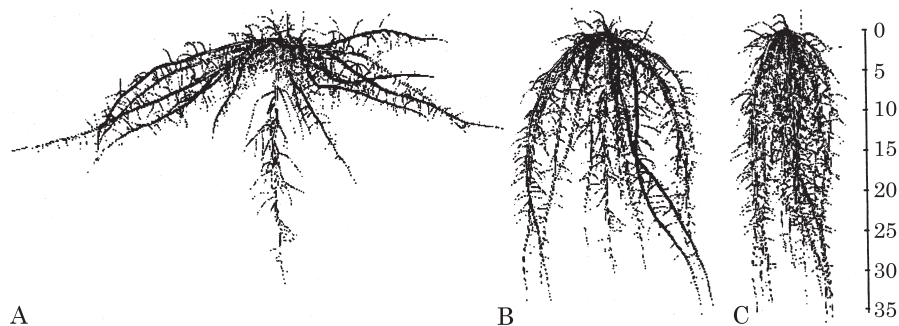


FIG. 2. Simulation of three common bean root systems after 320 h of growth: shallow (A), intermediate (B) and deep (C). Reference axis in cm.

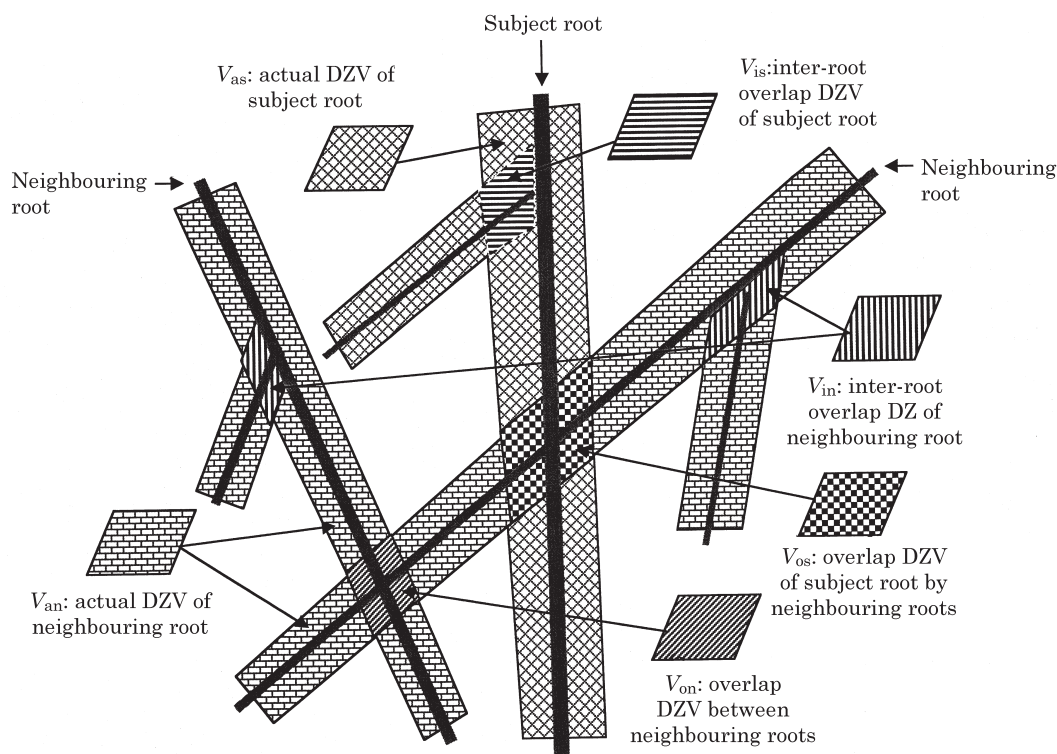


FIG. 3. Components of the depletion zone volume (DZV). Overlapping volume due to competition within and between root systems is shown. The different components are utilized to calculate the inter-plant root competition (see Materials and Methods).

root system. The basic algorithm of the program is similar to that of the previous program *DepZone* (Lynch *et al.*, 1997), which calculates the radius of the depletion zone around root segments and then estimates the volume of soil depleted by the entire system (as in Fitter *et al.*, 1991). The nutrient depletion zones of the system were represented as volume elements (voxels) within the depletion cylinder. Duplicated voxels, representing the overlapped volume, were then subtracted and the depletion volume without overlapping (actual depletion zone volume) was estimated. The new subprograms not only calculate the depletion zone of a single root system but also the overlapped depletion zone volume in the multiple root system.

Indices for evaluating inter-plant root competition and nutrient uptake by several root systems

In this study we used plant competition indices as a measure of the degree to which the below-ground niche of a plant is shared by other plants. In a previous study, competition for phosphorus among roots within a single root system was calculated as the percentage of the overlapped depletion volume over the actual depletion volume (Ge *et al.*, 2000). In this study, this is defined as intra-plant root competition (C_{IPR}). Similarly, inter-plant root competition for P (C_{IPR}) in the multiple root system is quantitatively expressed as:

$$C_{IPR} = \frac{V_{os}}{V_{as}} 100 \quad (1)$$

where V_{os} is the overlapping depletion zone volume of the subject root system with the neighbouring root systems and V_{as} is the actual depletion zone volume of the subject root system (Fig. 3).

To compare the relative importance of inter-plant to intra-plant root competition, the ratio of inter-plant root competition to intra-plant root competition (R_{MIC}) was calculated:

$$R_{MIC} = \frac{C_{IPR}}{C_{IR}} \quad (2)$$

To estimate the total competition for the whole assembly of competing root systems, total root competition (C_{TR}) was calculated as follows:

$$C_{TR} = \frac{(V_{os} + V_{on}) + (V_{is} + V_{in})}{V_{as} + V_{an}} \quad (3)$$

where V_{os} and V_{as} are the same as above; V_{on} is the overlapping depletion zone volume between neighbouring roots; V_{is} and V_{in} are the overlapping volumes of the subject and the neighbouring roots, respectively; and V_{an} is the actual depletion zone volume of the neighbouring roots (Fig. 3).

The expected uptake in competition as a fraction of the uptake by the root system in isolation (U) was calculated as:

$$U = \frac{V_{as}}{V_{as} + (0.5V_{os})} 100 \quad (4)$$

The above four indices quantify inter-plant root competition from different perspectives. The index C_{IPR} quantifies the decrease in explored soil volume due to competition with roots from neighbouring plants. R_{MIC} shows the relative importance of root competition from neighbouring plants compared with root competition within the subject plant. C_{TR} describes the total amount of root competition occurring when root competition both within plants and among plants is considered. U shows how uptake is affected by competition, by comparing the depletion zones of an isolated plant and a plant competing with its neighbours.

Changes in root gravitropism

To study the effects of root gravitropism on root competition, three root models were generated: shallow, intermediate (Carioca) and deep (Fig. 2). This range of gravitropism represents the natural genetic variation found in common bean (Bonser *et al.*, 1996). The three root models were generated by changing the gravitropic coefficient in *SimRoot*, which is a vertical vector that represents the tendency of roots to grow toward gravity (Lynch *et al.*, 1997). The three root systems had identical root length, biomass and topological branching patterns.

Variations in P diffusion coefficient, number of neighbours and distance between plants

We simulated soils with three D_e values: 1×10^{-7} , 1×10^{-8} and $1 \times 10^{-9} \text{ cm}^2 \text{ s}^{-1}$. The range of soil D_e for P employed in this study covered fully the range of values found in the field by Schenk and Barber (1979). The highest value of D_e is close to that found in an Aquic Argiudoll and the lowest to a Typic Udipsamment (Schenk and Barber, 1979). A constant distance of 3 cm between plants (comparable to inter-plant spacing in bean monocultures) was used for these simulations. The effect of the distance between neighbouring plants was evaluated specifically by comparing root competition of plants located from 1 to 9 cm apart (Fig. 4). These simulations were performed in soils with a D_e value of $10^{-8} \text{ cm}^2 \text{ s}^{-1}$ and using Carioca as a root model.

Phosphorus uptake by multiple root systems

Phosphorus uptake by a set of root systems was calculated by multiplying the actual depletion zone volume and the soil phosphorus supply capacity. Here, the phosphorus supply capacity is the amount of phosphorus per mm^3 of depletion zone that the soil can provide to the plant. In a previous paper (Ge *et al.*, 2000), we estimated and experimentally validated the supply capacity values for three phosphorus levels (low, medium and high). By using these figures, we simulated two soils: soil A, with homogeneous phosphorus availability, and soil B, with stratified phosphorus availability (greater phosphorus availability at the surface). In these simulations we assumed a D_e for P of $1 \times 10^{-8} \text{ cm}^2 \text{ s}^{-1}$.

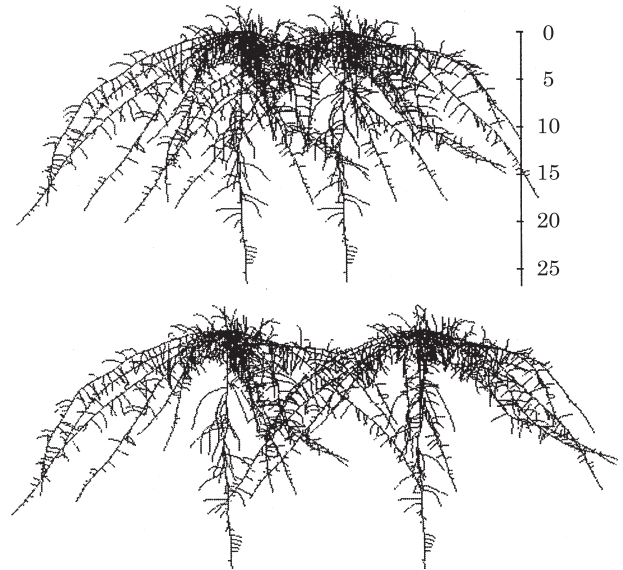


FIG. 4. Two competing Carioca (intermediate) root systems with different distances between plants (axis shown in cm).

Assumptions

To simplify the modelling process, the following assumptions were made:

First, depletion zone volumes were calculated from the diffusion coefficient of a particular nutrient in the soil. The radius of the depletion volume is expressed as:

$$R_{dz} = r + 2\sqrt{D_e t} \quad (5)$$

where R_{dz} is the radius of the depletion zone around the root, measured from the root centre; r is the radius of the root segment; D_e is the diffusion coefficient of the ion in the soil; and t is the time period of root growth (Nye and Tinker, 1977; Barber, 1995, see specifications also in Ge *et al.*, 2000). Each root segment had its own value of t . The root was assumed to be explicitly located in the centre of the soil cylinder around the root segment. Because the soil volume occupied by one root cannot be explored by another root, the root radius (r) was included in the calculus of the overlap of depletion volumes. Second, water and other nutrients do not interact with phosphorus to affect inter-plant root competition. Third, diffusive nutrients in overlapping depletion zones are shared equally by competing root segments. Fourth, all parts of the root system are active in P uptake and have a rather constant P uptake capacity; this has been observed in bean seedlings (Rubio, Sorgona and Lynch, unpubl. res.). Fifth, to estimate phosphorus uptake, it was assumed that all available phosphorus present in the depletion volume is taken up by the roots.

Each simulation model was replicated five times by changing the seed of the random number generator used to drive stochastic processes in the growth of each root system, resulting in roots with the same overall gravitropic coefficient but slightly different architecture (for graphical representation of example simulated replicates see Nielsen

et al., 1997 or Ge et al., 2000). This variation represents phenotypic variation of roots of the same genotype and also the influence of soil heterogeneity on root architecture. Data were statistically processed using ANOVA. All simulations ran for 320 h.

RESULTS

Effect of competition on the radial distribution of basal roots

Neither phosphorus supply nor inter-plant competition affected the radial distribution of basal roots (Table 1). In addition, we measured the length of the projected root length (Fig. 1) from roots inside and outside the 'target area'. Differences in length of the projected root would be an indicator of differences in basal root angle. There was no difference between projected root length inside (mean \pm s.e. = 7.0 ± 0.74 cm) and outside (7.8 ± 0.54 cm) the 'target area'. These results indicate that the general pattern of root architecture is the same in both isolated and competing plants. In terms of our simulations, this permits us to (1) evaluate inter-plant competition by overlapping root systems having similar geometry as individual root systems, and (2) compare the extent of root competition within plants (i.e. intra-plant root competition) and between neighbouring plants (i.e. inter-plant root competition).

Competition between contrasting genotypes under field conditions

No clear tendencies were detected in the total number of root intersections in the whole profile (Fig. 5), which suggests that the root systems of both genotypes were about the same size. In agreement with previous studies in controlled conditions (Liao et al., 2001), genotype G19833 concentrates most of its roots in the topsoil, whereas DOR 364 distributes them more homogeneously with depth (Fig. 5). Only slight differences in shoot biomass accumulation were observed among genotypes when they were cultivated as monocultures (Fig. 6). When the genotypes were intermixed (competition treatment), the shallow-rooted one (G19833) had the highest amount of accumulated biomass in both phosphorus treatments.

Effect of root gravitropism

To observe the effects of root gravitropism on competition, we simulated root systems differing in architecture but using a standard phosphorus diffusion coefficient (10^{-8} cm² s⁻¹) and a standard distance between the subject and neighbouring root systems (3 cm, which corresponds with a typical in-row inter-plant spacing in bean monocultures). Root gravitropism had a significant effect on inter-plant root competition (Table 2). The three highest values of inter-plant root competition corresponded to competition

TABLE 1. Percentage of roots in the 90° quadrant closest to the neighbouring plant as affected by genotype (BAT 477 and DOR 364), competition (no competition, competition with a plant of the same genotype, and competition with a plant of a different genotype) and P supply (low, medium and high)

Genotype	Low P			Medium P			High P		
	No Competition	Competition		No Competition	Competition		No Competition	Competition	
		w/same genotype	w/different genotype		w/same genotype	w/different genotype		w/same genotype	w/different genotype
BAT 477	29.1	24.6	36.3	20.7	22.6	31.5	27.0	24.0	28.6
DOR 364	33.0	24.0	32.5	17.3	29.3	29.6	32.4	25.2	23.3

For details in the procedure see Fig. 1. Data were statistically analysed to test the hypothesis that the mean = 25. In all cases the *t*-tests performed were significant at $P < 0.01$.

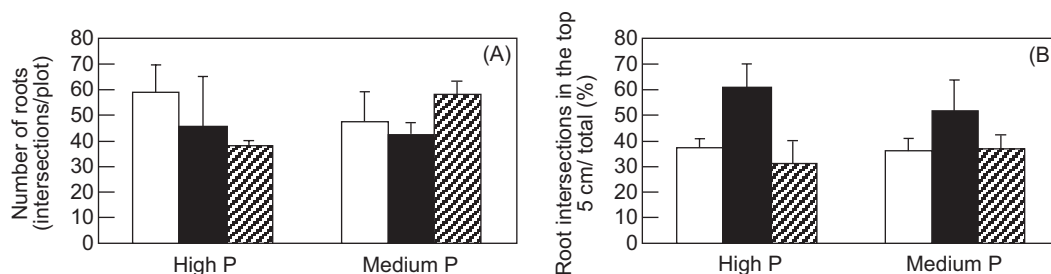


FIG. 5. Total number of intersections of thick roots on a trench dug 10 cm away from the stem of two bean genotypes contrasting in root architecture (A). No roots were observed 35 cm below the soil surface. Proportion of those intersections in the first 5 cm of the soil (B). DOR 364 (□; Deep, monoculture), G 19833 (■; Shallow, monoculture), DOR 364 + G 19833 (▨; Competition).

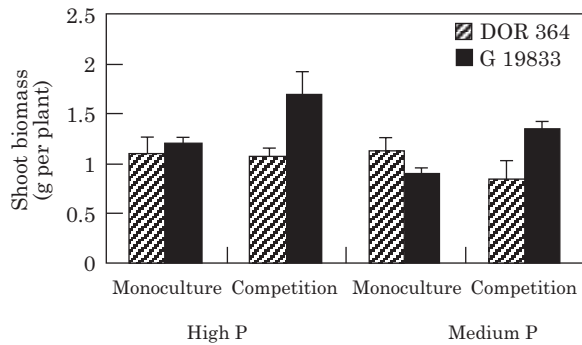


FIG. 6. Shoot biomass accumulation for two common bean genotypes contrasting in root architecture after 17 d of growth in fertilized and unfertilized field plots. Interplant spacing was 5 cm within a row, and rows were far enough apart to avoid shading among plants in different rows.

among root systems with the same architecture. Of these the shallow-shallow combination had the highest inter-plant root competition, followed by deep-deep. The most contrasting combination, deep-shallow, had the least inter-plant root competition, being 57 % lower than the shallow-shallow combination (Table 2). U values, which represent the expected uptake in competition as a fraction of the uptake by the root system in isolation, ranged between 94.7 and 97.8 %. The highest U values were found in root combinations with low inter-plant competition.

The ratio of inter-plant root competition to intra-plant root competition (R_{MIC}) shows the relative contribution of both components of below-ground competition to total root competition (Table 2). Inter-plant root competition was much lower than intra-plant root competition as indicated by R_{MIC} values lower than 1 in all combinations. Inter-plant root competition values represented only 21 to 56 % of intra-plant root competition (Table 2), which indicates that the overlap among roots of the same plant was greater than the overlap among roots of neighbouring plants. As observed for inter-plant root competition, the

highest values of R_{MIC} were observed in treatments in which roots of the same type competed. Total root competition (C_{TR}) values, which reflect the sum of inter- and intra-plant below-ground competition, ranged from 21.1 to 26.1 %. In a previous study we observed that deep root systems have the highest intra-plant root competition (Ge *et al.*, 2000). Accordingly, combinations which included this root architecture showed a high total root competition.

Effect of diffusion coefficient for phosphorus

As we observed earlier for intra-plant root competition (Ge *et al.*, 2000), the soil P diffusion coefficient (D_e) dramatically affects inter-plant root competition (Fig. 7). Varying D_e changed root competition more than three-fold (Fig. 7), and the effects of root gravitropism were intensified in soils with a high value of D_e . Comparing the different root types, the shallow and deep systems experienced slightly more competition than the intermediate system (Fig. 7). Whereas inter-plant root competition increased as the diffusion coefficient (D_e) increased, the relative proportion of inter-plant and intra-plant competition (R_{MIC}) did not. This means that the soil diffusion coefficient affected both inter-plant and intra-plant root competition in approximately the same proportion. The intermediate root system had the lowest values of R_{MIC} , indicating a lower incidence of inter-plant root competition in this root type. Total root competition (C_{TR}) responded to D_e in the same manner as did individual inter-plant root competition (Fig. 7). U values were higher at lower levels of D_e , and at all levels of D_e the intermediate root system had the highest values of this parameter.

Effect of the distance between neighbouring root systems

The primary effect of increasing the distance between neighbouring root systems was to decrease the inter-plant root competition of the subject root system (Fig. 8). Inter-plant root competition decreased greatly as the inter-plant

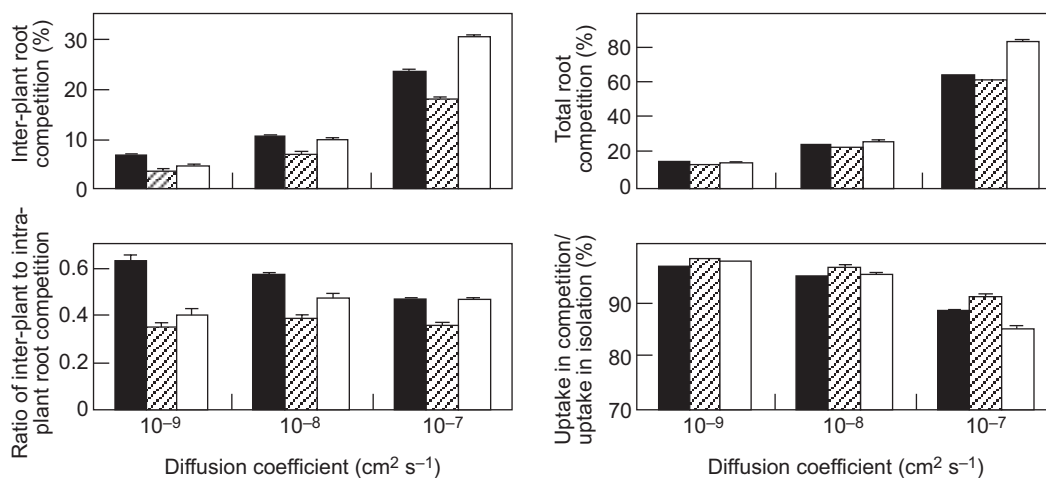


FIG. 7. Inter-plant root competition, ratio of inter-plant root competition to intra-plant root competition and total root competition as affected by soil diffusion coefficient and root architecture [shallow (■), intermediate (▨) and deep (□)]. The distance between subject roots and neighbouring roots was 3 cm. Each plant competes with a neighbour of the same root type. Data are means of five replicates \pm s.e.m.

TABLE 2. Inter-plant root competition (C_{IPR}), ratio of inter-plant root competition to intra-plant root competition (R_{MIC}), total root competition (C_{TR}) and ratio of uptake in competition to uptake in isolation (U) as affected by root architecture (shallow, intermediate and deep) and type of competition (all combinations of root architecture)

	Subject Root			
	Neighbouring root	Shallow	Intermediate	Deep
Inter-plant root competition (%)	Shallow	10.53 (0.24)	5.71 (0.12)	4.42 (0.23)
	Intermediate	5.78 (0.39)	7.00 (0.17)	5.91 (0.21)
	Deep	4.61 (0.21)	5.45 (0.35)	9.80 (0.32)
Ratio of inter-plant root competition to intra-plant root competition	Shallow	0.56 (0.01)	0.31 (0.00)	0.21 (0.02)
	Intermediate	0.32 (0.02)	0.38 (0.01)	0.29 (0.01)
	Deep	0.25 (0.01)	0.3 (0.01)	0.46 (0.02)
Total root competition (%)	Shallow	23.95 (0.00)	N.A.	N.A.
	Intermediate	21.13 (0.00)	22.07 (0.00)	N.A.
	Deep	21.35 (0.00)	22.32 (0.00)	26.07 (0.01)
Ratio of P uptake in competition to P uptake in isolation (%)	Shallow	94.73 (0.00)	97.14 (0.00)	97.78 (0.00)
	Intermediate	97.10 (0.00)	96.5 (0.00)	97.04 (0.00)
	Deep	97.76 (0.00)	97.27 (0.00)	95.09 (0.01)
ANOVA results	C_{IPR}	R_{MIC}	C_{TR}	U
Factor (d.f.)	F value			
Subject (2)	47.99***	20.29***	57.60***	47.99***
Neighbour (2)	50.15***	7.97**	68.15***	50.15***
Subject x neighbour (4)	64.00***	70.53***	66.21***	64.00***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

C_{IPR} and R_{MIC} were measured in the subject root. Means and s.e. (in parentheses) are shown in the upper section of the table and ANOVA results in the lower section. NA, Not applicable.

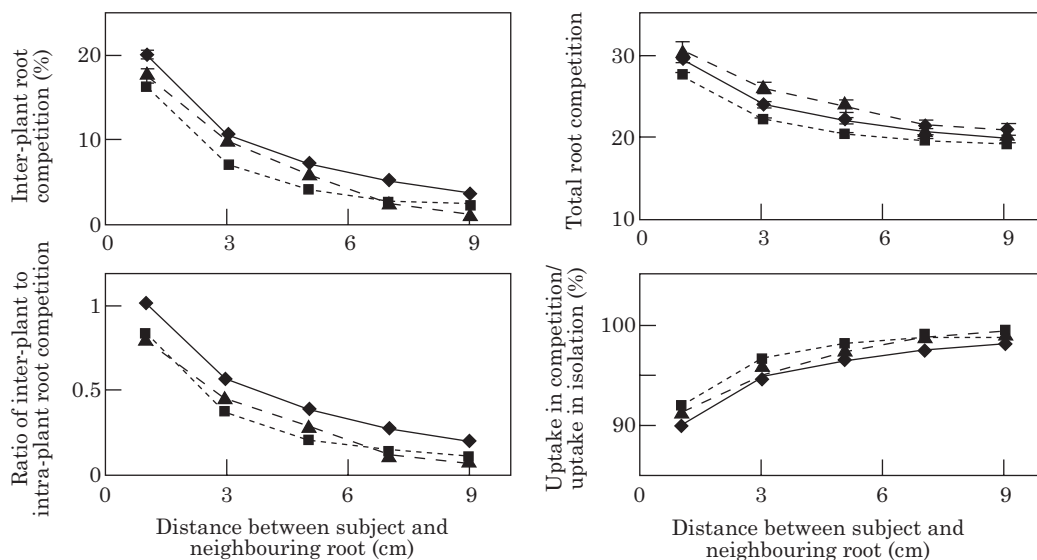


FIG. 8. Inter-plant root competition, ratio of inter-plant root competition to intra-plant root competition and total root competition as affected by the distance among competing roots and root architecture [shallow (—◆—), intermediate (—■—) and deep (—▲—)]. Data are means of five replicates \pm s.e.m.

distance increased from 1 to 9 cm (16 to 20% at 1 cm spacing vs. 1 to 5% at 9 cm spacing). A significant effect of root gravitropism was observed on inter-plant root competition: the shallow and deep root systems had higher values of competition than the intermediate ones. When plants were 9 cm apart, there was almost no effect of

competition on nutrient uptake: U ranged from 98.1 (shallow) to 99.2% (deep root system). At 1 cm, U was consistently lower: 89.9, 91.8 and 91.2% for the shallow, intermediate and deep root types, respectively. Because intra-plant root competition is not affected by the distance between plants, the ratio of inter-plant to intra-plant root

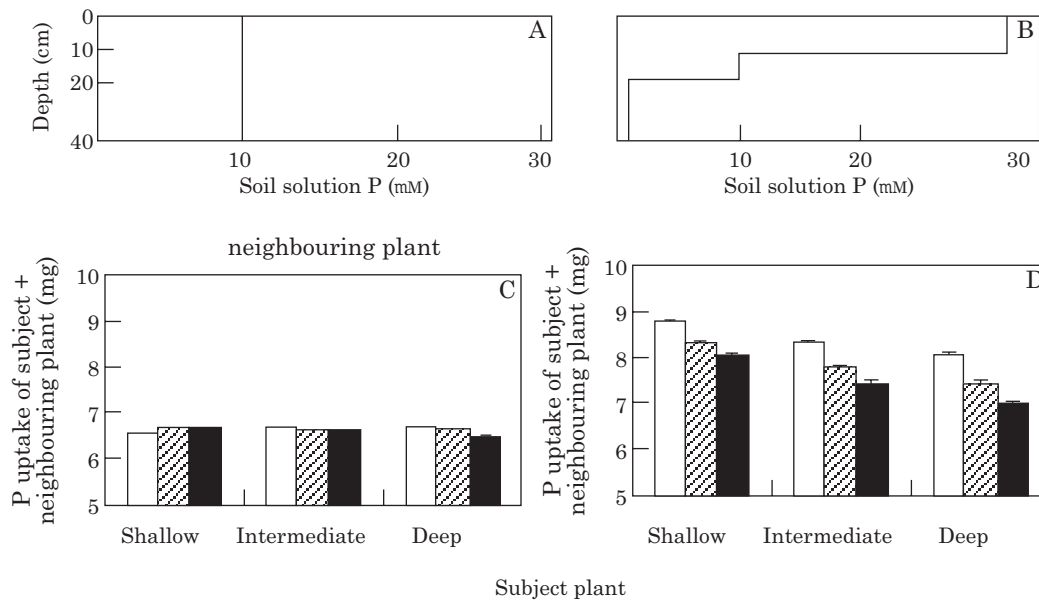


FIG. 9. Two simulated soil profiles, showing homogeneous (A) and heterogeneous (B) soil phosphorus distribution; and P uptake of subject plant and subject plus neighbouring plant as affected by root architecture [shallow (\square), intermediate (\square) and deep (\blacksquare), soil type [homogeneous (C) and heterogeneous (D)] and competition (all combinations of root architectures). Data are means of five replicates \pm s.e.m.

competition (R_{MIC}) and total root competition C_{TR} also decreased as distance increased (Fig. 8).

Inter-plant root competition increased almost linearly as the number of neighbouring roots increased. Inter-plant root competition was 5 % when the subject root had just one neighbouring plant (3 cm apart, $D_e = 10^{-8} \text{ cm}^2 \text{ s}^{-1}$) but increased to 20 % with four neighbouring plants.

Phosphorus uptake

Root architecture affected phosphorus uptake by competing root systems in both homogenous and heterogeneous soils (Fig. 9). Heterogeneous distribution of soil phosphorus intensified competition among plants. In general, pairs of root systems in stratified soil could take up about twice as much phosphorus as those in homogeneous soil. When comparing pairs of competing roots with the same architecture in heterogeneous soils, we observed a clear advantage of the shallow root system over the intermediate and deep root systems. Pairs of shallow root systems acquired more phosphorus than pairs of intermediate root systems, which in turn had a greater P acquisition than pairs of deep root systems (Fig. 9). On the other hand, when pairs of competing plants with contrasting root architecture were compared, we observed that the inclusion of a shallow root system always increased total P uptake.

DISCUSSION

Competition for below-ground resources occurs among neighbouring plants and also among roots of the same plant. In a previous report we observed that the proportion of the root system which is not active in nutrient uptake due to intra-plant root competition increases as a consequence of root age, greater phosphorus diffusivity, and increased

root depth (Ge *et al.*, 2000). The combined effect of these factors resulted in a 20-fold range of variation in intra-plant root competition. In the present study, we extend these results by analysing the overlap of soil volumes explored by roots of neighbouring plants. Competition among roots of different plants basically depends on whether they coexist spatially and temporally and how nutrient demands of competing plants are segregated temporally (Casper and Jackson, 1997). Since the presence of neighbours did not affect the general pattern of radial distribution of basal roots (Table 1), in this study we assume that plants have basically the same root architecture in both competitive and non-competitive (i.e. isolated plants) conditions; this appears to be a valid assumption for common bean seedlings. The experiment reported in Table 1 shows the response of the root system as a whole, on a broad scale. To investigate the effects of root competition on root trajectories on a finer scale further experiments could be made.

Root architecture combinations which result in low inter-plant competition are more efficient for total phosphorus acquisition, as they tend to minimize the overlap of depletion zones of adjacent roots. This is an inefficient process since an overlapped volume is explored by several roots at the same time, which ultimately reduces the phosphorus acquired per unit of resources invested below-ground. We observed that combinations of roots of the same architecture resulted in more intense inter-plant competition. Of these, the deep-deep and shallow-shallow combination showed the most intense competition (Table 2). Whereas the combination of two deep roots resulted in an overlap of almost 10 %, when the same deep root system competed with a shallow root system the overlap was reduced by almost half. Considering a group of plants as a whole, a combination of roots of contrasting architecture would be the most efficient way to capture below-ground resources.

In this study we simulated root growth for 320 h after germination. We propose that root competition in older plants would follow the same trend as described here, although it would be more intense. In annual dicot root systems, the basal roots comprise the skeleton or scaffold upon which the rest of the root system develops through lateral branching. Because the basal root system begins growing immediately after the taproot elongates (Lynch and van Beem, 1993), the initial gravitropic curvature of the basal roots will continue throughout vegetative development, and will determine the depth and architecture of a significant portion of the root system. In the field experiment we observed that gravitropic sensitivity after 6 d was consistent with root growth patterns after 4 weeks, implying that root architecture is determined in the early stages of growth and that the architectural characteristics (such as shallowness) persist throughout the vegetative phase of development (see also Liao et al., 2001).

It has been suggested that the average nutrient concentration in the soil is less important in determining the competitive success of a plant than the small-scale heterogeneity of nutrient availability (Jackson and Caldwell, 1989; Campbell et al., 1991). In light of this hypothesis, resource capture in homogeneous soils would be defined by the effective total root length (after discounting the overlap zones) of the whole ensemble of roots. In environments where the limiting resource is heterogeneously distributed in the soil, co-localization of root foraging and resource distribution would be an important factor in resource capture. Our results support these predictions for relatively immobile nutrients such as phosphorus: the outcome of competition was quite different in homogeneous and heterogeneous soils, although they had almost the same total phosphorus content (Fig. 9). Whereas phosphorus uptake from homogeneous soil was only slightly affected by the root architecture of competing plants, root architecture exerted a large influence on phosphorus uptake in heterogeneous soils. In these soils, the shallow root system was able to acquire the greatest amount of phosphorus, regardless of the architecture of the competing root system. Therefore, phosphorus uptake depended primarily on the presence of roots where the resource was at its highest concentration, in this case the topsoil. Results from our model are consistent with the field data obtained in China. Whereas in monocultures both genotypes accumulated almost the same amount of biomass, when they were grown in competition the shallow-rooted genotype surpassed the deep-rooted genotype in terms of shoot biomass.

Increased D_e , and thus greater phosphorus mobility, led to increased inter-plant root competition (Fig. 7). This indicates that plants growing in soils with higher D_e suffer more intense competition with their neighbours, although it does not necessarily imply that such plants acquire fewer diffusion-mobile nutrients. Higher values of D_e enlarge the radius of the depletion volume around a root axis, thereby increasing the likelihood that adjacent root segments will have overlapping depletion zones and will therefore compete. However, a wider radius of depletion also exploits an increased volume of soil and therefore potentially more nutrients. On the other hand, we observed that the effects of

D_e on inter-plant competition paralleled those of D_e on intra-plant competition, so that the proportion of the two types of competition remained relatively constant with changing D_e . Data shown in Fig. 7 are also relevant to the effects of root competition for nutrients other than phosphorus. Since D_e values for potassium, molybdenum, zinc, manganese and ammonium are usually within the range analysed here for phosphorus (Barber, 1995), our results could be extended to these nutrients.

Mycorrhizal symbiosis enhances the capacity for phosphorus acquisition of most higher plants. Mycorrhizal fungi can absorb and translocate P to the host plant from soil outside the root depletion volume. Several studies have attempted to study the interactions between mycorrhizal colonization and inter-plant competition (e.g. Zobel et al., 1997; Moora and Zobel, 1998). In terms of inter-plant competition, mycorrhizal activity would act mainly as a factor to increase the actual depletion volume, thereby increasing the probability of overlap with the nutrient depletion zones of neighbouring plants. To our knowledge, published literature does not offer unambiguous data that would permit the quantitative estimation of the influence of external hyphae on root depletion zones of competing plants. However, we note that in common bean, root architecture is related to P acquisition efficiency independently of mycorrhizal effects (Lynch and Beebe, 1995; Bonser et al., 1996). A possible explanation for this is that mycorrhizal colonization and the consequent P uptake derived from this process occur near host roots. In other words, a shallower root system may also have shallower hyphal foraging.

Our simulations do not consider root competition for water, which is likely to be an important component of below-ground competition in many environments. Niklas has elegantly shown how the evolution of contrasting shoot architectures may be understood as co-optimizing solutions for several environmental constraints (Niklas, 1995). Undoubtedly the same is true for root architecture: co-optimization of root architecture for mechanical support, acquisition of diffusive nutrients, and acquisition of water (and with water, soluble nutrients), will have to be considered for a fuller understanding of the functional importance of root architecture. However, in the case of common bean, basal root gravitropism is related to genetic adaptation to low P soils in both competitive and non-competitive situations in the tropics (Bonser et al., 1996; Rubio, Liao, Yan and Lynch, unpubl. res.), where most beans are grown, and where nutrient limitations are generally more serious than water limitations.

Our results indicate that for young plants, competition among roots of the same plant is larger than competition among roots of neighbouring plants. To our knowledge, this is the first report to quantify this phenomenon in 3D. Intra- vs. inter-plant root competition is a valid comparison in agricultural settings, where 'fitness' is related to the productivity of an entire stand of plants. In natural settings or with intense weed competition, intra-plant competition has very different implications for plant performance than does inter-plant competition. Nutrients acquired by the roots of a neighbouring plant are not available to the subject plant, and could be used to the detriment of a subject

plant by a competitor, whereas nutrients acquired by roots of the subject plant will obviously benefit the subject plant, regardless of which root acquired them. Intra-plant root competition is detrimental to the subject plant to the extent that limiting resources invested in root foraging have been wasted. We have shown that a significant amount of the carbon assimilated by common bean plants is used for root production and maintenance under phosphorus stress (Nielsen *et al.*, 1994). Intra-plant competition may be important for plant adaptation to phosphorus stress by determining the efficiency with which carbon invested in root foraging is converted to phosphorus acquisition. A comparable analysis is possible considering the efficiency of phosphorus invested in root foraging (Koide *et al.*, 1999), especially in view of the observation that P invested in root production is scarcely remobilized to the rest of the common bean plant under P stress (Snapp and Lynch, 1996). Architectures that produce large intra-plant root competition may be advantageous in circumstances in which intense niche colonization is useful, or in which a significant amount of root loss is expected from abiotic or biotic stress.

In both natural and agricultural ecosystems, plants must compete with their neighbours to acquire below-ground and above-ground resources. Below-ground competition appears to be more complicated since: (1) whereas plants have to share only one above-ground resource (light), below-ground competition is for water and 16 essential nutrients; (2) the availability of each of these resources is affected by many distinct factors in a highly heterogeneous environment; (3) a direct relationship between the size of the plant and above-ground competitive ability exists, whereas no single factor explains below-ground competitive ability so precisely; and (4) above-ground competition and factors that affect it can be assessed more accurately than below-ground competition (Casper and Jackson, 1997). For example, shading among neighbouring plants is a principal factor controlling above-ground competition and one which can be easily quantified by measuring incident radiation. On the contrary, overlap of depletion volumes, the equivalent of shading in root competition, cannot be simply and accurately measured in experiments with real plants (Robinson, 1991). By using *SimRoot*, we quantified how root gravitropism, soil diffusion coefficient, soil heterogeneity, distance between neighbouring plants, and the number of competing plants influence the overlap of depletion volumes of neighbouring plants. Inter-plant root competition represented only 21 to 56 % of competition within the same plant (Table 2). In agroecosystems, inter-plant root competition can be manipulated through management practices (for example, by altering the distance between plants), but intra-plant competition cannot. Basically, intra-plant root competition is an unavoidable consequence of root growth and branching. Since it is greatly affected by root architecture, and because several species show a large genetic variation in root architecture (O'Toole and Bland, 1987; Bonser *et al.*, 1996), genetic selection for roots which experience less intra-plant competition may be a means of increasing the efficiency of nutrient acquisition.

ACKNOWLEDGEMENTS

This research was supported by USDA/NRI grants 97-0053 and 1999-00632, NSF grant 9602255 and BARD grant IS-2949-97R to JPL and the National Key Basic Research Special Funds of China grant (G1999011700) and the National Natural Science Foundation of China Grant (39925025) to XY.

LITERATURE CITED

- Aerts R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-feedbacks. *Journal of Experimental Botany* **50**: 29–37.
- Baldwin JP. 1976. Competition for plant nutrients in soil; a theoretical approach. *Journal of Agricultural Science (Cambridge)* **87**: 341–356.
- Barber SA. 1995. *Soil nutrient bioavailability: a mechanistic approach*. New York: Wiley-Interscience.
- Bonser AM, Lynch JP, Snapp S. 1996. Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytologist* **132**: 281–288.
- Callaway RM, Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**: 1958–1965.
- Campbell BD, Grime JP, Mackey JML. 1991. A trade off between scale and precision in resource foraging. *Oecologia* **87**: 532–538.
- Casper BD, Jackson RB. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**: 545–570.
- Clausnitzer V, Hopmans J. 1994. Simultaneous modeling of transient three-dimensional root growth and soil water flow. *Plant and Soil* **164**: 299–314.
- Diggie AJ. 1988. ROOTMAP—a model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant and Soil* **105**: 169–178.
- Firn RD, Digby J. 1997. Solving the puzzle of gravitropism—has the lost piece been found? *Planta* **203**: S159–S263.
- Fitter AH, Stickland TR, Harvey ML, Wilson GW. 1991. Architectural analysis of plant root systems I: Architectural correlates of exploitation efficiency. *New Phytologist* **118**: 375–382.
- Ge Z, Rubio G, Lynch JP. 2000. The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. *Plant and Soil* **218**: 159–171.
- Hutchinson JMC. 2000. Three into two doesn't go: two-dimensional models of bird eggs, snail shells and plant roots. *Biological Journal of the Linnean Society* **70**: 161–187.
- Jackson RB, Caldwell MM. 1989. The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* **81**: 149–153.
- Jungk A, Claassen N. 1997. Ion diffusion in the soil-root system. *Advances in Agronomy* **61**: 53–110.
- Koide RT, Dickie IA, Goff MD. 1999. Phosphorus deficiency, plant growth and the phosphorus efficiency index. *Functional Ecology* **13**: 733–736.
- Liao H, Rubio G, Yan X, Cao A, Brown KM, Lynch JP. 2001. Effect of phosphorus availability on basal root shallowness in common bean. *Plant and Soil* **232**: 69–79.
- Lynch JP. 1995. Root architecture and plant productivity. *Plant Physiology* **95**: 7–13.
- Lynch JP, Beebe SE. 1995. Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability. *HortScience* **30**: 1165–1171.
- Lynch JP, Nielsen KL. 1996. Simulation of root system architecture. In: Waisel Y, Eshel A, Kafkafi U, eds. *Plant roots: the hidden half*. New York: Marcel Dekker, 247–257.
- Lynch JP, van Beem J. 1993. Growth and architecture of seedling roots of common bean genotypes. *Crop Science* **33**: 1253–1257.
- Lynch JP, Epstein E, Läuchli A, Weigt G. 1990. An automated greenhouse sand culture system suitable for studies of P nutrition. *Plant Cell and Environment* **13**: 547–554.

- Lynch JP, Nielsen K, Davis RD, Jablokow AG. 1997. *SimRoot*: modeling and visualization of botanical root systems. *Plant and Soil* **180**: 139–151.
- Martin MPLD, Snaydon RW. 1982. Root and shoot interactions between barley and field beans when intercropped. *Journal of Applied Ecology* **19**: 263–272.
- Moora M, Zobel M. 1998. Can arbuscular mycorrhiza change the effect of root competition between conspecific plants of different ages? *Canadian Journal of Botany* **76**: 613–619.
- Nielsen KL, Lynch JP, Weiss HN. 1997. Fractal geometry of bean root systems: correlations between spatial and fractal dimension. *American Journal of Botany* **84**: 26–33.
- Nielsen KL, Lynch JP, Jablokow AG, Curtis PS. 1994. Carbon cost of root systems: an architectural approach. *Plant and Soil* **165**: 161–169.
- Niklas KJ. 1995. Morphological evolution through complex domains of fitness. In: Fitch WM, Ayala FJ, eds. *Tempo and mode in evolution: genetics and paleontology fifty years after Simpson*. Washington, DC: National Academic Press, 145–165.
- Nye PH, Tinker PB. 1977. *Solute movement in the soil-root system*. Berkeley: University of California Press.
- O'Toole JC, Bland WL. 1987. Genotypic variation in crop plant root systems. *Advances in Agronomy* **41**: 91–145.
- Pages L, Jordan MO, Picard D. 1989. A simulation model of the three-dimensional architecture of the maize root system. *Plant and Soil* **119**: 147–154.
- Pothuluri JV, Kissel DE, Whitney DA, Thien SJ. 1986. Phosphorus uptake from soil layers having different soil test phosphorus levels. *Agronomy Journal* **78**: 991–994.
- Robinson D. 1991. Roots and resource fluxes in plants and communities. In: Atkinson D, ed. *Plant root growth: an ecological perspective*. Oxford: Blackwell, 102–130.
- Schenk MK, Barber SA. 1979. Phosphate uptake by corn as affected by soil characteristics and root morphology. *Soil Science Society of America Journal* **43**: 880–830.
- Schenk HJ, Callaway RM, Mahall BE. 1999. Spatial root segregation: are plants territorial? *Advances in Ecological Research* **28**: 145–180.
- Schuurman JJ, Goedewaagen MAJ. 1971. *Methods for the examination of root systems and roots*. Wageningen: Centre for Agricultural Publishing and Documentation.
- Smethurst PJ, Comerford NB. 1993. Simulating nutrient uptake by single or competing and contrasting root systems. *Soil Science Society of America Journal* **57**: 1361–1367.
- Snapp SS, Lynch JP. 1996. Phosphorus distribution and remobilization in bean plants as influenced by phosphorus nutrition. *Crop Science* **36**: 929–935.
- Tilman D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton: Princeton University Press.
- Zobel M, Moora M, Haukioja E. 1997. Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. *Oikos* **78**: 202–208.